

## MECHANISMS OF SPATIAL COMPETITION OF *DISCINISCA STRIGATA* (INARTICULATA: BRACHIOPODA) IN THE INTERTIDAL OF PANAMA

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### ABSTRACT

The inarticulate brachiopod *Discinisca strigata* uniformly wins competitive interactions for space with other sessile epifauna in the intertidal of the Pacific Panamanian coast. This result is achieved through *D. strigata's* abilities to (1) metamorphose directly on the surface of bryozoan colonies, (2) maintain a pool of particle-depleted water around most of the shell, (3) abrade underlying calcareous epifauna with the shell, eroding them to the level of the substrate, and (4) abrade the tissues of adjacent sponges and bryozoan zooid buds with modified lateral setae. (1) and (2) are allowed by a reversal of the described flow patterns in brachiopods and the possession of a functional siphon formed from modified setae; (3) is possible because the inorganic component of the brachiopod's shell, calcium phosphate, is much harder than calcium carbonate. Three of these mechanisms are not available to articulate brachiopods and the fourth is apparently not exploited, which may explain differences in competitive abilities between the two classes.

### INTRODUCTION

Despite the considerable paleontological importance of brachiopods, their ecology is poorly known; only about 350 species are extant, but on some hard substrates brachiopods are a prominent component of the sessile fauna. All living brachiopods except lingulids and a few articulates (Neall, 1970; Richardson and Watson, 1975a, b) are permanently attached by the pedicle or by cementation of one valve (Thayer, 1981). As immobile epifauna, brachiopods have inhabited hard substrates, presumably competing for space with other epifauna, since the Lower Cambrian. Colonial animals such as sponges and bryozoans are generally superior competitors when competing with solitary animals (Jackson, 1977; but see Greene and Schoener, 1982), and recent studies have clarified the competitive relationships (see Jackson, 1983) and mechanisms (Buss and Jackson, 1979; Buss, 1981) of these and other sessile epifauna, but most studies of brachiopod ecology have concentrated on the demography and population structure of articulates (see Thayer, 1981; Witman and Cooper, 1983). Only Doherty (1979) has addressed how articulate brachiopods fare in competition with other sessile organisms for substrate space; no work has addressed the competitive abilities of inarticulates.

The present study of *Discinisca strigata* grew out of continuing work on brachiopod hydrodynamics (LaBarbera, 1977, 1981), so the samples were not specifically collected to investigate spatial competition. However, description of the competitive relationships and mechanisms implied by evidence from these specimens seems warranted because these results contrast sharply with the reported competitive abilities and mechanisms of solitary animals in other phyla.

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## MATERIALS AND METHODS

Rock fragments were collected from overhangs and crevices in the mid-intertidal at Punta Patilla, Panama. The ecology (Reimer, 1976a, b) and competitive relationships of some epibionts (Buss, 1980, 1981) at this site have been described. Specimens were held briefly in tanks at the Smithsonian Tropical Research Institute, Galeta, Panama, before being hand-carried to Chicago in a styrofoam cooler. On arrival, the fauna were acclimated to the water in the holding tanks over a 3-hour period; all animals survived transport. The animals were fed a mixed culture of diatoms supplemented with commercial bakers yeast when diatom cultures ran low.

Each rock was mapped at 3× using a Wild M5A stereo microscope and camera lucida; all epifauna were outlined and living fauna distinguished from remnants of epibionts. The rocks were also scanned at 6× and 12× to detect overlooked fauna (primarily juvenile *D. strigata*) and to clarify the nature of faunal interfaces observed at 3×. When work on *D. strigata*'s behavior and hydrodynamics was complete, the rocks were submerged in a container of sea water, aliquots of 7% MgCl<sub>2</sub> added until the animals no longer responded to disturbance, and buffered formalin added to yield a 10% solution. The rocks were later resubmerged in sea water and each *D. strigata* removed from its substrate by carefully cutting the pedicle. Any epifauna revealed were recorded on the maps of the rocks.

Areas were measured from the maps using an Apple II+ microcomputer and digitizing pad. All areas reported are the coverage as seen from a viewpoint perpendicular to the plane of the substrate. Where large epibionts were themselves covered by epizoans, the encrusted area was counted twice; such instances represent a minor fraction of the total reported coverage.

## RESULTS

*General*

Rock areas varied from 21 to 116 cm<sup>2</sup>. The fractional area covered by epifauna averaged 49%; free space varied from 32–74%. *D. strigata* covered 2–26% of the surfaces; bryozoans, primarily *Antropora tinctoria*, covered 5–38%. Other major epibionts included serpulids (2.5–29%), spirorbids (0.01–7.3%), and sponges (0.5–8.2%). The most densely encrusted rock is reproduced in Figure 1; coverage data is summarized in Table I. Single individuals of *Isognoman jamus* and *Hipponix panamensis* were also found, but are omitted from this tabulation.

A total of 194 *D. strigata* were seen; 17 were juveniles under 2 mm in diameter. In contrast to the northern Gulf of California (Paine, 1962), the *D. strigata* at Punta Patilla commonly occurred in clusters (animals separated by less than 2 mm) of from two to over a dozen animals; solitary individuals were a minority. One third of the *Disinisca* (17% of the total valve area) bore epizoans, primarily bryozoans and spirorbids, with occasional *D. strigata*, serpulids, and small sponges.

*Behavior of the living animals*

All *D. strigata* opened within 45 min after transfer to the tanks; all appeared healthy. Details of *D. strigata*'s flow patterns will be described elsewhere (LaBarbera, in prep.), but note that flow directions are the reverse of articulates (LaBarbera, 1981); water enters the shell anteriorly and exits through the lateral gapes (Fig. 2). Paine (1962) noted this pattern, but it has been subsequently overlooked.

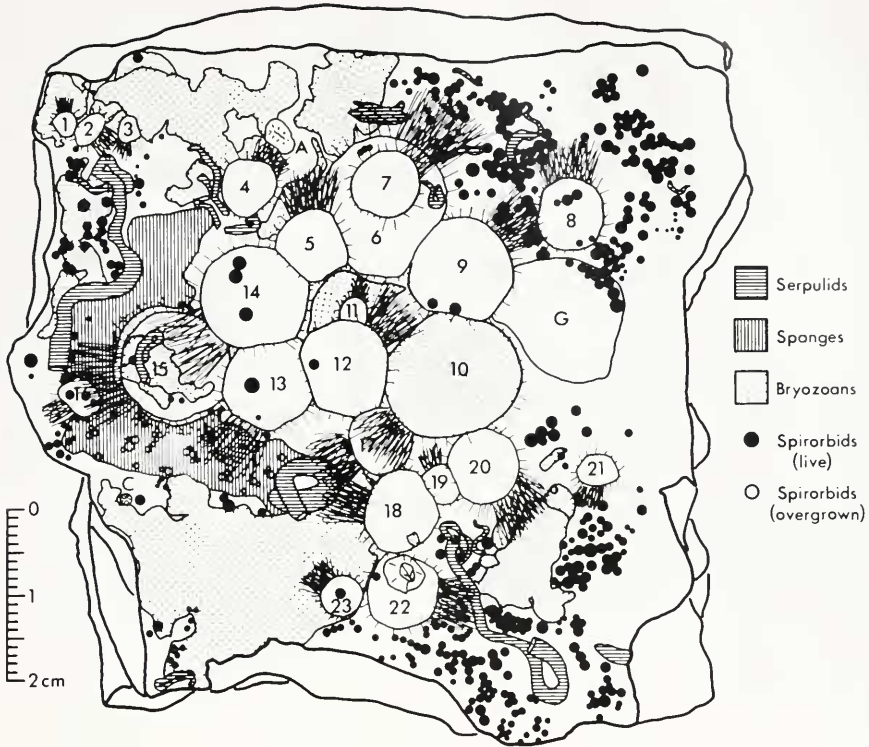


FIGURE 1. Camera lucida drawing of rock 6 (Table 1). All *D. strigata* are numbered. Note the clear zone separating brachiopod 15 from the surrounding sponge and the inhibition of the bryozoan encrusting it by brachiopod 14's anterior setae. Brachiopods 6 and 22 bear a *D. strigata* (number 7) and barnacle, respectively. The interactions occurring in the vicinity of brachiopods 1-4, 15-16, and 17-23 are shown in greater detail in Figure 4. Bryozoan colonies (*Antropora tincta*) are marked by stippling, sponges by vertical hatching, serpulids by horizontal hatching, and spirorbids by circles (solid if exposed, open if overgrown). More complex patterns indicate overgrown. C = solitary coral, A = anemone, G = gastropod (*Crepidula striolata*).

*D. strigata*'s densely packed anterior setae function as a siphon (Fig. 2). These setae are very long (comparable in length to the valves) and bear fine lateral processes (Fig. 3) which mechanically interlock and decrease the mean size of the spaces between the setae. No detectable flow occurs between the anterior setae except near their most distal tips; incurrent water is drawn from well in front of the animal, usually in a plane above the substrate. The lateral setae are about half the length of the anterior setae and much less densely packed; their lateral processes (Fig. 3) are short, stout, and thorn- or hook-like. The posterior setae bear similar ornamentation, but are much shorter than the lateral setae.

When disturbed (and at irregular intervals with no obvious stimulus), the animals rapidly closed their valves and initiated a stereotyped behavior pattern:

(1) With the valves nearly closed, the dorsal valve was rotated clockwise and counterclockwise through a total arc of 60-120°. This movement rubbed the lateral setae of the dorsal mantle over and past the ventral setae. The setal siphon was distorted by this movement but remained patent.

TABLE I

*Epizoans on the rocks collected at Punta Patilla, Panama*

| Rock                            | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11    |
|---------------------------------|------|------|------|------|------|------|------|------|------|------|-------|
| Total area (cm <sup>2</sup> )   | 11.6 | 20.8 | 45.0 | 50.2 | 51.5 | 52.9 | 61.8 | 66.1 | 68.7 | 72.3 | 116.4 |
| Epizoans (% cover) <sup>1</sup> |      |      |      |      |      |      |      |      |      |      |       |
| <i>Discinisca</i>               | 9.8  | 11.8 | 3.2  | 8.7  | 13.0 | 26.0 | 1.8  | 16.8 | 19.6 | 7.7  | 9.9   |
| <i>Antropora</i>                | 12.8 | 1.1  | 6.9  | 23.8 | 14.5 | 22.5 | 37.7 | 1.7  | 0.6  | —    | 7.3   |
| <i>Onychocella</i>              | —    | 18.5 | —    | 1.6  | 0.9  | —    | —    | 6.6  | —    | 3.3  | —     |
| <i>Microporella</i>             | —    | —    | —    | 2.4  | —    | —    | —    | —    | —    | 1.6  | —     |
| Sponges                         | —    | —    | 7.0  | 1.9  | 1.2  | 6.9  | 6.4  | 8.2  | 6.9  | 0.5  | 2.1   |
| Serpulids                       | 2.5  | 4.8  | 4.2  | 9.2  | 9.4  | 4.4  | 5.7  | 10.1 | 14.1 | 28.8 | 3.7   |
| Spirorbids                      | 1.3  | 3.3  | 0.01 | 6.9  | 5.6  | 5.2  | 7.3  | 3.9  | 1.2  | 4.2  | 5.5   |
| <i>Crepidula</i>                | —    | —    | 5.8  | —    | —    | 3.0  | 0.3  | —    | —    | 0.2  | 10.5  |
| Vermetids                       | —    | —    | —    | —    | —    | —    | —    | 0.3  | —    | 2.9  | 3.7   |
| Barnacles                       | —    | —    | 0.3  | 0.4  | 0.2  | 0.3  | —    | —    | 0.4  | 0.2  | 0.5   |
| Corals                          | —    | —    | —    | —    | —    | 0.03 | —    | —    | —    | 4.4  | 0.1   |
| Anemones                        | —    | —    | —    | —    | —    | 0.19 | —    | —    | —    | —    | —     |
| Oysters                         | —    | —    | —    | —    | —    | —    | —    | —    | —    | 2.6  | —     |
| Fragments                       | —    | —    | 7.6  | —    | —    | —    | —    | —    | —    | —    | —     |
| Free space                      | 73.6 | 60.6 | 65.1 | 45.3 | 55.4 | 31.5 | 40.8 | 52.4 | 57.3 | 43.7 | 56.8  |

<sup>1</sup> Blank entries indicate that no representatives of that group were found. The entries labeled *Discinisca*, *Antropora*, *Onychocella*, *Microporella*, and *Crepidula* are the brachiopod *D. strigata*, the bryozoans *A. tineta*, *O. alula*, and *M. umbracula*, and the gastropod *C. striolata* respectively; the fragments listed are fragments of cemented oyster valves and the bases of the sessile gastropod *Hipponix panamensis*.

Values listed for the epizoans and for free space are percentages of the total projected area of the rock surface.

(2) When the dorsal valve returned to its normal alignment with the ventral valve, the valve margins were clamped together tightly and both valves were rotated as a unit through a total arc of 60–150°.

(3) On return to rest position, the valve margins were clamped tightly to the substrate. After a few seconds to several minutes, the valves returned to a position slightly elevated above the substrate and the animal slowly reopened.

#### *Spatial competition between Discinisca and other epifauna*

Numerous examples of apparent spatial competition between *D. strigata* and the other epifauna, particularly sponges and bryozoans, were noted. Although sponges on these rocks had overgrown serpulids, spirorbids, and bryozoans, only once was there any suspicion of a sponge overgrowing a *D. strigata*; the shell found under this sponge was small (approximately 5 mm diameter), and so badly eroded that it could not be positively identified even to phylum. Most of the sponges were thin, encrusting forms which grew up to the lateral or anterior margins of the brachiopods only when hidden in irregularities in the substrate; where the substrate lacked relief, the brachiopods were surrounded by a clear zone approximately the length of the lateral setae (Figs. 1, 4a). Whenever these sponges grew within 2–3 mm of the posterior margin of a *Discinisca* they exhibited arrested growth and a distinct ridge produced by vertical growth. Four large, thick sponges grew beside or around brachiopods; a distinct clear zone devoid of sponge occurred around the brachiopods except near





FIGURE 2. A live *D. strigata*, actively pumping. The anterior setae are interlocked to form a functional siphon; water is drawn into the animal anteriorly and exits laterally. The catheter tube is filled with a 1:3 mixture of milk and sea water.

the shell anterior. Near the substrate, this zone was equal or slightly smaller in width than the length of the setae, but, a few millimeters above the substrate, the sponges overhung the brachiopods' shells (Fig. 4a). The sponges never actually touched the shell; the two were usually separated by 2–4 mm.

Thirty-six *A. tinctoria* colonies abutted or surrounded brachiopods; in 12 of these, zooids adjacent to the brachiopod had produced a distinct ridge in the colony through frontal budding. Near the anterior or posterior valve margins, this ridge was less than 2 mm from the brachiopod, but near the lateral margins, the ridge occurred at the tips of the lateral setae. In most cases, the location of the bryozoan's growing edge indicated that the brachiopod had been overtaken by a colony expanding its spatial coverage (Fig. 4b). Three other *A. tinctoria* colonies partially encrusted a brachiopod whose posterior half was brushed by the tips of a second brachiopod's anterior setae; where brushed by the setae, these colonies exhibited arrested growth and a ridge 2–3 zooids thick (e.g., Fig. 1, animals 14 and 15).

Undercutting and wear was apparent on epifauna adjacent to or overlapped by brachiopods. Where bryozoans extended beneath brachiopods (23 of the 177 adult brachiopods), zooids near valve margins were visibly worn and some had been bisected (Fig. 5). The 7 spirorbids near the edges of brachiopods (7 cases) were similarly damaged; one fourth to three fourths of each whorl was worn nearly to the substrate (Fig. 4a, c, 6a). Ten serpulids (Fig. 4b), two vermetids, and two corals were also worn, although the damage to these animals was not as dramatic as for bryozoans or spirorbids and the individuals had survived.

When the brachiopods were removed, evidence of past interactions was found beneath the valves (Fig. 4). All spirorbids (24) found under *D. strigata* (13 animals)

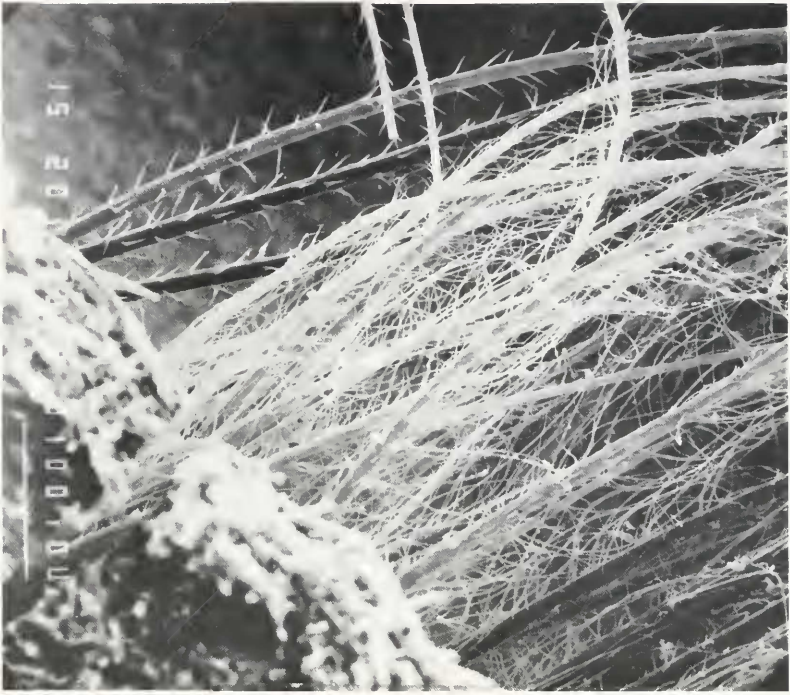


FIGURE 3. SEM micrograph of the anterior (AS) and lateral (LS) setae of *D. strigata*. The anterior setae bear long, thread-like lateral processes that entangle in forming the anterior siphon; the processes of the lateral and posterior (not shown) setae are short, stout, and thorn-like. Scale bar = 100  $\mu\text{m}$ .

were highly worn; most were so eroded that the entire tube was exposed (Fig. 4a, c, 6b). All 18 colonies of sheet-like bryozoans hidden by the brachiopods' valves (Fig. 4a) were extensively worn as were the 9 colonies of "runner" (Jackson, 1979) morphology (Fig. 4c). [Runner-like bryozoans are early colonists but poor competitors (Jackson, 1979); they occurred on the free surface of the rocks only twice.] The 10 fragments of serpulid tubes (under 7 brachiopods) were all highly worn and polished (e.g., Fig. 4c). The undamaged shell of a dead juvenile (1.7 mm diameter) *D. strigata* was found attached beside the pedicle of a second, larger animal. Remains of epifauna were even found underlying the brachiopods' pedicles. Such cases included nine sectioned spirorbids under the pedicles of eight *D. strigata* (Fig. 4c), six worn sheet-like bryozoan colonies (6 brachiopods), four of which underlay the entire pedicle attachment (Fig. 4c), six worn runner-like bryozoans (2 brachiopods), and three worn and polished serpulid tube fragments (2 brachiopods). Three juvenile *D. strigata* (1.2–2.3 mm diameter) were attached to the frontal walls of zooids in the center of living *A. tinctoria* colonies; thus these animals' pedicles were also underlain by bryozoans and metamorphosis must have occurred directly on the living colony.

#### DISCUSSION

The rocks studied were small and may not be a representative sample of the habitat; only 617.3 cm<sup>2</sup> of this habitat was investigated. Static samples are not ideal

for reconstructing competitive relationships, but this approach has been used previously and yields qualitatively valid results (Buss, 1980, 1981; Quinn, 1982; Russ, 1982; Jackson, 1983). Despite these limitations, some aspects of *D. strigata's* ecology seem clear.

*D. strigata* is the spatial dominant on only 3 of the 11 rocks investigated, even though it dominates in competitive interactions. However, only in the case of serpulids on rock 10 does another sessile, solitary animal dominate the space. Before speculating on why *D. strigata* does not dominate to a greater extent, those features that mediate its offensive and defensive functions should be clarified.

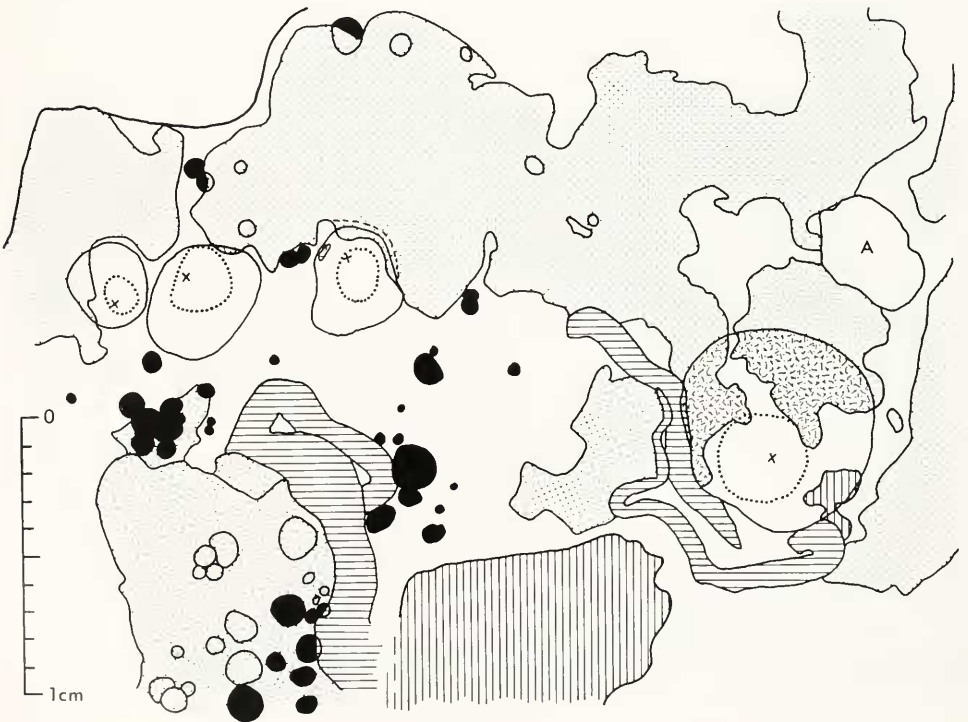
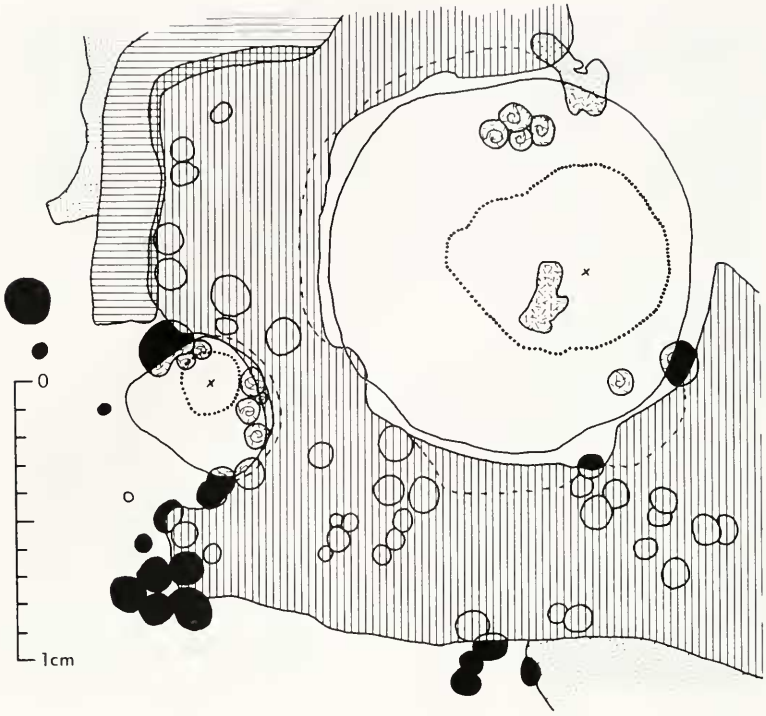
#### *The role of water flow patterns*

Utilization of the anterior setae to form an incurrent siphon may be crucial to *Discinisca's* success in competitive interactions. Since bryozoan zooids expel filtered water towards the substrate, and brachiopods and bryozoans probably exploit the same size fraction of particles (*cf.*, Winston, 1976; Jorgensen *et al.*, 1984), the water near the surface of a bryozoan colony would be devoid of food for a newly-metamorphosed brachiopod; the low local Reynolds number (see Vogel, 1981) implies poor mixing. Three juveniles were seen which had metamorphosed on living bryozoan colonies; if the presence of a single bryozoan colony underlying the entire pedicle is acceptable evidence for a brachiopod's metamorphosis on a living colony, then seven such cases occurred. *D. strigata's* functional siphon allows juveniles to draw water from above the bryozoan's lophophores, permitting feeding and ultimately allowing it to usurp space occupied by the colony. For larger juveniles and adults, the ability to draw water from well above the substrate will minimize the effects of particle depletion (see Buss and Jackson, 1981; Jackson, 1983) by other suspension feeding epifauna.

Since filtered water exits the brachiopods through the lateral shell gapes at low speeds (LaBarbera, in prep.), water on the sides of the brachiopods will be particle-depleted. This nutritionally depleted water might act as a barrier to bryozoan encroachment if colonies grow towards nutritionally favorable microenvironments (Winston, 1976). Since sponges can filter submicron sized particles (Reiswig, 1971) while brachiopods poorly retain particles smaller than 2  $\mu\text{m}$  (Jorgensen *et al.*, 1984), feeding interference by *D. strigata* might seem unlikely. However, particles smaller than 1  $\mu\text{m}$  constitute less than 5% of the diet of sponges (Reiswig, 1971). The growing edge of sponges quickly becomes functionally independent of the main body (Simpson, 1963); if locally available water is depleted of particulates, local growth of the sponge will be repressed. This explanation is consistent with the arching morphology of the larger sponges growing in the brachiopods' vicinity; certainly the brachiopods' other competitive mechanisms (see below) could have no direct effect on portions of the sponges growing more than a few millimeters above the substrate. A similar situation has been described for bryozoans (Buss, 1980, 1981).

#### *Mechanical interference with other epifauna*

The cessation of substrate-level growth of sponges and bryozoans at a distance from the brachiopods equal to the lengths of the lateral and posterior setae implies a direct role of the setae in preventing overgrowth. *D. strigata's* lateral and posterior setae are robust and equipped with stout, thorn-like processes (Fig. 3). *Discinisca's* stereotyped rotation on closure sweeps these setae through an arc around the shell





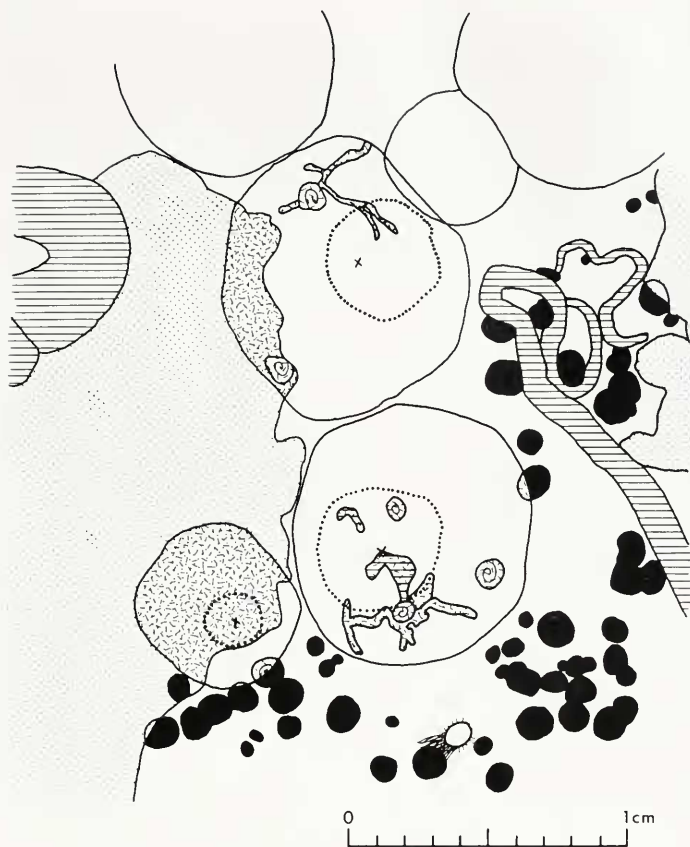


FIGURE 4. Abrasion of epifauna beneath *D. strigata*. The brachiopods' valve margins are outlined, but the valves are drawn as if transparent; setae have been omitted for clarity. Dotted lines outline the pedicle border at its attachment to the substrate; "X" marks the projected position of the brachial valve apex. Epifauna are identified with the conventions of Figure 1; abraded epifauna are indicated by an overlay of short, random hatching.

(a) Encrusting sponge surrounding two *D. strigata* (15 and 16 of Fig. 1). A zone devoid of sponge surrounds each animal near the substrate (dashed line); further from the substrate, the sponge arches over the brachiopods but never touches the shells. Note the abraded bryozoan colony under the pedicle of one brachiopod (right) and abraded spirorbids under both animals; eroded regions end abruptly at the shell margins. The sponge under the anterior margin of the right hand brachiopod lies in a depression in the rock's surface.

(b) Brachiopods 1-4 (left to right) of Figure 1. The anterior and left sides of brachiopod 1 (far left) are elevated due to the slope of the rock beneath the animal; the underlying bryozoans are alive. In contrast, animals 2-4 lie flat on the surface and underlying bryozoans have been abraded to the colony basis. The apparent overgrowth of brachiopod 3 by an *Antropora tinctoria* colony results from the perspective. Near the substrate, the colony margin (dashed line) is located at the tips of the lateral setae; the colony has undergone extensive frontal budding and begun to arch over the shell, but nowhere comes within 1 mm of the brachial valve. As in (a), the sponge under brachiopod 4 (far right) lies in a depression.

(c) Brachiopods 18, 22, and 23 of Figure 1. Abraded bryozoans and spirorbids underly all three animals. The eroded "runner" bryozoans under brachiopods 18 and 22 were not visible elsewhere on the rock, and presumably had been overgrown by other epifauna. The bryozoan on the left underlies brachiopod 23's entire pedicle attachment, implying that this brachiopod metamorphosed directly on the colony's surface. The juvenile *D. strigata* in the lower portion of the drawing was too small to be distinguished in Figure 1.



FIGURE 5. SEM micrograph of a bryozoan colony (*Antropora tincta*) adjacent to a *D. strigata*. The brachiopod's valve margins are indicated by broken lines; note that several zooids adjacent to the brachiopod have been bisected (arrows) and that the colony has been eroded down to its basis beneath the brachiopod. Scale bar = 100  $\mu\text{m}$ .

and mechanically inhibits sponge and bryozoan growth by directly damaging their tissues.

The growing edge of sponges is initially thin (Ayling, 1983) and lacks spicular or fibrous reinforcement (Simpson, 1963). Although the rate of spatial coverage may increase dramatically where the sponge has been disturbed, absolute rates of coverage are maximally 6.98  $\text{mm}^2/\text{cm}$  perimeter/day (Ayling, 1983). Given the frequency with which *D. strigata* sweeps the vicinity with its setae and the vulnerability of sponge tissues, such low expansion rates are easily nullified.

Newly budded bryozoan zooids are weakly calcified (Ryland, 1970); contrary to the usual pattern (Jackson, 1983), here the bryozoan's actively growing edge is more vulnerable than the fully calcified regions where growth is arrested. *Antropora tincta* exhibits frontal budding when growth is blocked (Buss, 1980, 1981; Jackson, 1983); for colonies around *D. strigata*, the only available agent for blockage is the brachiopod's setae. As noted above, frontal budding can be induced in *A. tincta* by the anterior setae of adjacent brachiopods. Since these setae are longer (thus exerting smaller forces at their tips) and lack the spines of the lateral and posterior setae, these bryozoans will be highly vulnerable to the disturbance imposed by the latter.

Numerous eroded epizoans occurred under the brachiopods' ventral valves, although no abrasion of the valve itself was seen. The edge of the ventral valve is the most likely abrasive agent as evidenced by: (1) ground and polished regions on adjacent serpulids, vermetids, and corals, (2) bisected spirorbids and bryozoans where overlapped by a *D. strigata*, (3) a dead but undamaged *D. strigata* juvenile beside the pedicle of

an adult, and (4) the clearance I observed between the central regions of the ventral valve and the substrate. The inorganic component of *D. strigata*'s valves is about 75%  $\text{Ca}_3(\text{PO}_4)_2$  (Jope, 1965), a mineral with a Mohs hardness of 5.0; calcite and aragonite, the inorganic skeletal components of most calcareous epifauna, have hardnesses of 3.0 and 3.5–4.0, respectively. Thus the preferential abrasion of the epifauna arises from the much harder mineral comprising the brachiopod's valves. Whether the minute periostracal spines of *D. strigata* (Williams and Mackay, 1979) play any part in this abrasion is unknown. The characteristically abraded epifauna present beneath adult brachiopods' pedicles implies that this mechanism is effective even in juveniles.

### *Brachiopods as spatial competitors*

Since up to three-fourths of the space on these rocks was unoccupied, it might be argued that discussion of spatial competition is moot. However, from the perspective of sessile epibionts, the only relevant space is that bordering the individual or colony; if this space is contested and lost, the loser will incur a cost in terms of potential growth and thus reproductive potential. The numerous observed overgrowths of epifauna by sponges and bryozoans imply that competition for space does occur; the contests inferred for *D. strigata* also represent local competition for space around individuals.

If *D. strigata* dominates in both direct and indirect (Woodin and Jackson, 1979) competitive interactions, why has it not monopolized the space on these rocks? Although no definitive answer is available, the possibilities appear to be limited to physical disturbance, predation, or failure to secure space as fast as it opens up. This study can offer no insight into the frequency of physical disturbance, and the only evidence of predation was the presence of small (less than 500  $\mu\text{m}$  diameter), straight-sided boreholes in three *D. strigata*, all of which were still alive. No scars on the rocks or fauna indicating removed animals were noted. However, a poor ability of co-opt newly opened space is implied by the determinate growth of adult *D. strigata* (see Jackson, 1979) and the low frequency of juveniles. All juveniles were approximately the same size and thus probably represent a single recruitment episode; if recruitments are annual and all of this magnitude, it would take over ten years (assuming no mortality) to build up the observed adult population. Even if *D. strigata* is the competitive dominant, its domination of space is thus likely to be a protracted exercise. If this argument is valid, this system's dynamics follow Greene and Schoener's (1982) "fixed lottery" model.

*D. strigata* is effective at defending space against encroachment, can co-opt space at metamorphosis that colonial animals previously occupied, and can acquire additional space as it grows – abilities unexpected in sessile, solitary animals (Jackson, 1983). Brachiopods are generally presumed (e.g., Jackson *et al.*, 1971; Thayer, 1981) to be competitively inferior, but the evidence for this view is meager and restricted to articulate brachiopods. Thayer (1981) reports that articulate brachiopods are poor competitors for space when competing with mobile animals such as mussels. In the present study *D. strigata* usually occupied more space than the only mobile epibiont present, *Crepidula striolata* (Table I). Doherty (1979) has documented frequent overgrowth of juveniles of the articulate brachiopod *Terebratella inconspicua* by both bryozoans and sponges. In contrast, of the 17 live juvenile *D. strigata* seen in the present study, none appeared to be in any danger of overgrowth; the only juvenile which had unequivocally lost such an interaction had been smothered by an adult *D. strigata*.



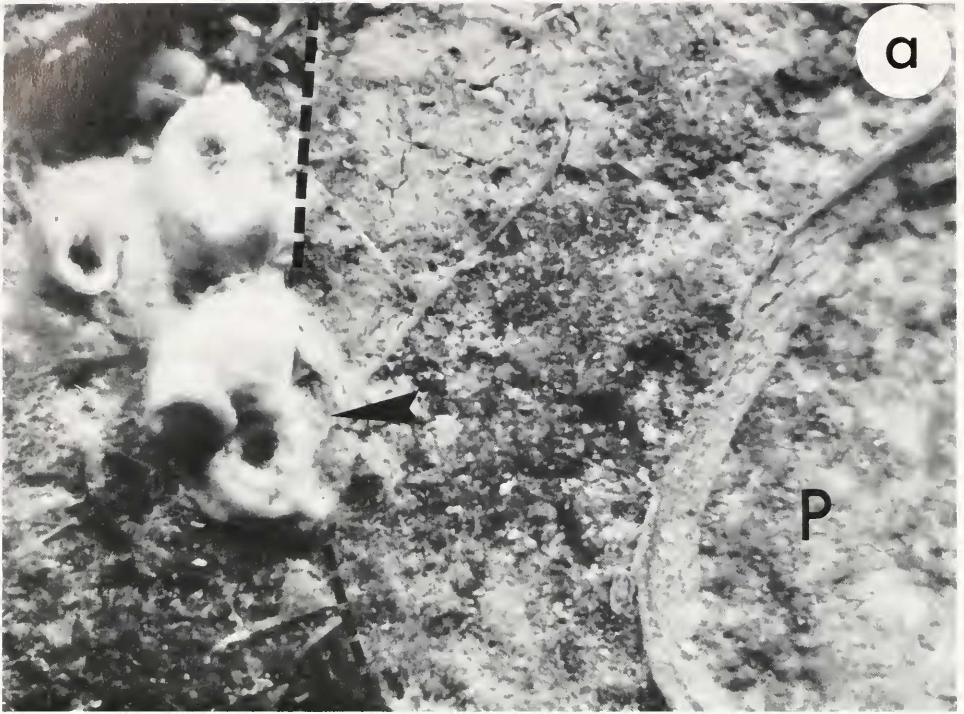


FIGURE 6. Abrasion of spirorbids by the ventral valve of *D. strigata*. Both photographs are of dried specimens; scale bar = 5 mm. (a) A spirorbid, partially overlapped by a *D. strigata*, with a portion of one whorl abraded to the substrate (arrow). The margin of the ventral valve of the brachiopod is indicated by the broken line; a portion of the cuticle covering the pedicle (P) can be seen to the right. (b) A spirorbid



Differences in competitive abilities between the articulates studied by Doherty (1979) and the inarticulates studied here are likely due to a suite of characters. Pedunculate brachiopods' mobility on the pedicle makes them a functionally unstable substrate for overgrowth; both LaBarbera (1977) and Doherty (1979) note that this mobility helps articulate brachiopods avoid overgrowth. In all articulates, however, the pedicle foramen is marginal; the more central foramen in *D. strigata* affords greater protection for the pedicle and insures that the entire shell margin, including regions adjacent to the pedicle, sweep through a sizable arc when the animal rotates, thus inhibiting epifaunal growth at a greater distance from the shell than is possible for articulates.

Rotation of the valves in *D. strigata* mechanically abrades surrounding epibionts through the actions of both the shell and the setae; neither mechanism is well developed in articulate brachiopods. *Discinisca's* distinctively ornamented setae are unique; the setae of both lingulids (Blochmann, 1900; Storch and Welsch, 1972; Orrhage, 1973; Westbroek *et al.*, 1980) and a variety of articulates (Gustus and Cloney, 1972; Orrhage, 1973) are simple straight shafts. Some articulates prune surrounding non-calcified epizoans with the shell during rotation (LaBarbera, 1977), but abrasion of calcified epifauna may not be possible; all articulates possess a calcium carbonate shell and any abrasion of calcareous epifauna would equally abrade the shell.

### General

The anterior incurrent/lateral excurrent flow in *D. strigata* has not been described for any other brachiopod, but I have observed similar patterns in the inarticulate *Crania californica* (LaBarbera, unpubl.). Given the paucity of work on living brachiopods, this pattern may be typical of the seven genera of acrotretid inarticulates.

The strong differentiation in length and ornamentation of the anterior, lateral, and posterior setae appears to be characteristic of the genus; Blochmann (1900) describes and figures similar setal structure and differentiation in *Discinisca lamellosa*. Blochmann (1900) does not mention flow directions through *D. lamellosa* or whether the anterior setae form a siphon, but he worked from preserved specimens where the setal siphon would be difficult to discern and information on flow directions unobtainable. Given the similarities between *D. strigata* and *D. lamellosa*, particularly the differentiation between the anterior and lateral setae and the similar shell compositions, *D. strigata's* mechanisms of competitive interaction are likely to be characteristic of the genus and may have been important in insuring the genus' success since it arose in the lower Jurassic (Rowell, 1965).

It is often possible to reconstruct competitive relationships among fossil epibionts (see, *e.g.*, Jackson, 1983). For fossil *Discinisca* preserved *in situ*, it should be possible to recognize the characteristic shell-generated abrasion of underlying calcareous epibionts, and careful observations on the distribution of epibionts might also produce evidence for setal abrasion.

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which was completely overlapped by a *D. strigata* and abraded to the point where nearly the entire tube has been opened. The brachiopod lay at an angle due to the slope of the underlying substrate; note the smooth bevel of the spiriferid's abraded surface. Conventions as in (a).

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